

Photoreceptor cells in chiton aesthetes

(Mollusca, Polyplacophora, Chitonidae)

Von F. P. Fischer

Zoologisches Institut der Universität München

Abstract

In the dorsal shell organs (the aesthetes) of three Polyplacophoran species photoreceptor cells have been found. Distally they have microvilli and sometimes cilia. These areas can be considered as rhabdomers. The middle part of the cell is filled with a modified agranular endoplasmic reticulum. It is supposed that photoreceptor cells are a regular part of the aesthetes and the basis in the evolution of the shell eyes.

1. Introduction

All Polyplacophorans studied so far possess small organs in their shells, the aesthetes. In some species eyes have also been found there in addition to the aesthetes (MOSELEY 1885, NOWIKOFF 1909). Several investigations showed that chitons react to light stimuli, whether they have eyes or not (AREY and CROZIER 1919, BOYLE 1972). Because no other possible light receptors have been found in the adult animals it is widely thought that the aesthetes are lightsensitive. But no special photoreceptor cell could be detected (KNORRE 1925, BOYLE 1974). Small cells which are situated in the central area of the aesthete terminating distally in short microvilli have been supposed to react to light.

An aesthete organ (Fig. 1) consists of a shaft, the megal aesthete, which terminates at the shell surface with a perforated cap. Clublike secretory cells are the most prominent structures in the aesthete. Laterally branching cells, the micraesthetes, form smaller caps at the shell surface. The megal aesthete is covered with thin wall cells. The aesthetes are innervated.

2. Methods

Pieces of the tegmentum containing aesthetes were fixed for electron microscopy in 5% chilled glutaraldehyde in phosphate buffer (pH 7,4) for two hours, decalcified in chilled 3% EDTA in phosphate buffer, dehydrated in ethanol and finally embedded in Durcupan. The sections were stained with uranyl acetate and lead citrate and examined with an Zeiss 9 S-2 electron microscope.

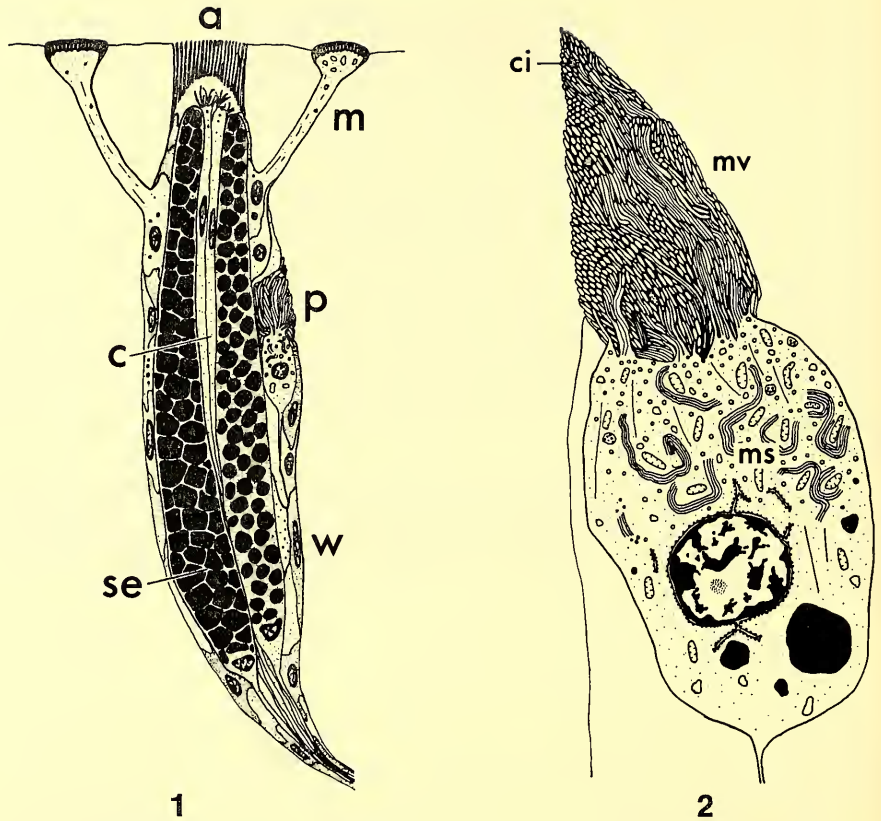


Fig. 1: Schematic diagram of an aesthete. se club-like secretory cell, c central cells, a apical cap, m microaesthete, p photoreceptor cell, w wall cells.

Fig. 2: Photoreceptor cell of *Acanthochiton fascicularis*, schematic drawing. mv microvilli, ci cilium, ms membraneous structures.

3. Results

In *Chiton olivaceus* Spengler and in *Acanthochiton fascicularis* L. as well as in the more primitively organized species *Lepidopleurus cajetanus* Poli well developed sensory cells lying in the periphery of the megalaesthete were found. In *Chiton olivaceus* these cells are situated more distally than in the other species, sometimes protruding laterally from the aesthete; in other aesthetes they may take most of the space in the middle-distal part of these organs.

Up to four of the described cells are present in one aesthete. Their structure is similar in the three species. The distal part consists of closely packed microvilli of a diameter between 50 and 350 nm (Fig. 2 and 3). Ciliary structures have not been found in *Chiton olivaceus*, although they are a regular feature in *Acanthochiton fascicularis*. *Lepidopleurus cajetanus* has a few at the most. The median cell region is filled with densely packed membraneous structures (Fig. 4). As these are

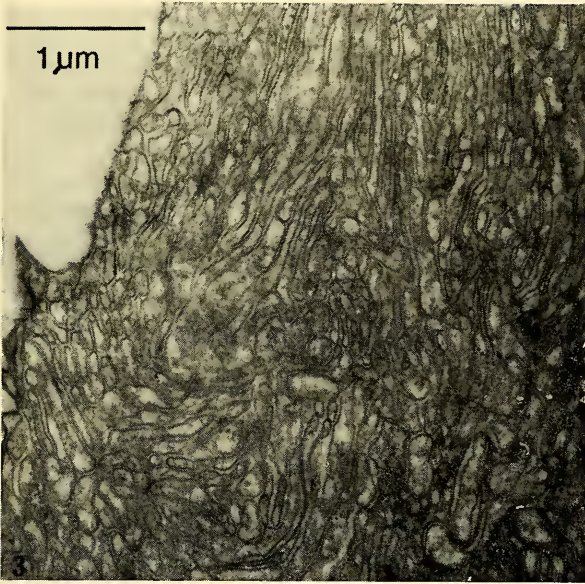


Fig. 3: *Chiton olivaceus*, photoreceptor cell, longitudinal section. Microvilli.

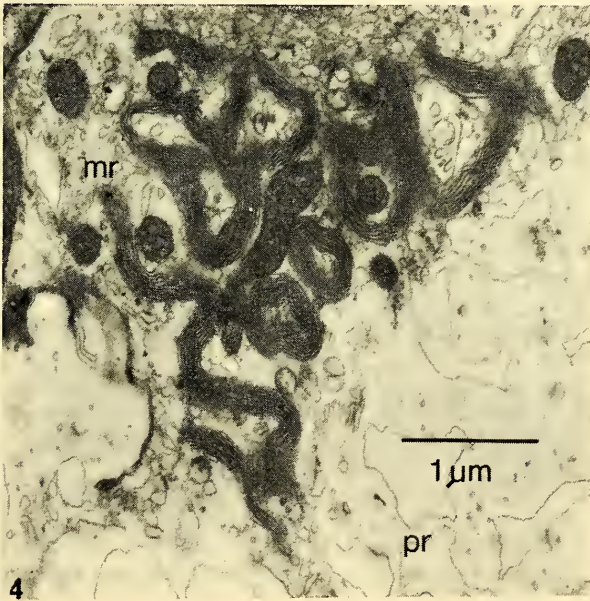


Fig. 4: *Chiton olivaceus*, photoreceptor cell, longitudinal section. Median (mr) and proximal (pr) cell region.

connected with the granular endoplasmic reticulum in some parts it is assumed that these structures are a specialised agranular endoplasmic reticulum. Most of the space between them is filled with numerous mitochondria and various vesicles. The proximal part of the cell around the nucleus with its prominent nucleolus shows scattered granules and often irregular regions of poor electron density. The cell has a process that might well be the axon.

In several Polyplacophoran species so-called intrapigmental eyes have been described (NOWIKOFF 1909). In these organs the tegmentum forms a small lense above a few photoreceptor cells which are situated in the same position in the aesthete as the described cells. There are also striking similarities with the visual cells of the extrapigmental shell eyes in *Onithochiton neglectus* Rodbrune (BOYLE 1969) as well as with the visual cells of other photoreceptors (RÖHLICH 1970, KERNEIS 1975) with regard to their ultrastructure. In our investigations only the described cells show differences in light- and darkadapted aesthetes. In *Chiton olivaceus* e. g. the microvilli membranes get thicker in the darkadapted animals. So these cells doubtless act as photoreceptors.

As these cells are found in all three species each one belonging to another of the three Polyplacophoran orders it is assumed that photoreceptor cells are a regular part of fully developed aesthetes except in cases in which shell eyes are present. In the case of the extrapigmental shell eyes the photoreceptor cells either dissociated from the aesthetes or they repressed the other cell types. From the situation in *Chiton olivaceus* one can get arguments for both alternatives; the comparison with the extrapigmental shell eyes of *Onithochiton neglectus* (BOYLE 1969) where sometimes aesthetes branch from the eyes' peduncles gives strong evidence for the first one. In the case of the intrapigmental eyes they remained at one side of the aesthete, where wall cells formed some pigment. *Acanthochiton fascicularis* and *Lepidopleurus cajetanus* represent the original situation; from aesthetes like those of *Chiton olivaceus* one can think an evolution either to extra- or to intrapigmental eyes. So the aesthetes of this species represent an intermediate state in the development of shell eyes.

4. Literature

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F. P. F i s c h e r, Zoologisches Institut der Universität
Luisenstr. 14, D-8000 München 2

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